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A CONSIDERATION OF CERTAIN PATHOLOGIC CONDITIONS IN AMBROSIA TRIFIDA

ALBAN STEWART

In two former publications (8, 9) the writer has shown certain similarities between the structure of gall and that of traumatic tissue. In one of these articles the structure of an insect gall was described and figured; in the other a fungus gall was given similar consideration. The structures involved in both of these galls were compared with the traumatic tissue of the same species of plant on which the galls occurred. Certain similarities in the structure of both of these galls led to some speculation as to what might result anatomically if the same species of plant were attacked by both a fungus and an animal parasite. Furthermore, what would result if both fungus and insect should exert their influence in a gall at the same time, and how would the changes caused by these different stimuli compare with the traumatic tissue of the plant on which the gall occurred?

I have been fortunate enough to secure material which illustrates the effects of these different combinations of stimuli. The stems of the great ragweed, *Ambrosia trifida* L., are sometimes infected by *Protomyces andinus* Lagh., causing large galls. The stems of the same plant are parasitized by *Papaipema nitela* Gn., which causes more or less pronounced swellings on the stem. Furthermore, it is quite often the case that both of these organisms are present in the same gall, and that both have evidently exerted an influence on its structure. Stems which have been wounded and subsequently healed are commonly found along roadsides. A single Protomyces gall was also found which had been wounded. The structure of the pathologic tissues arising from these various causes will be considered in this article.

GALL OF PROTOMYCES ANDINUS ON AMBROSIA TRIFIDA

In a neglected spot near the railroad track at Blue Mounds, Wisconsin, there is a thicket of *Ambrosia trifida* which is badly infected with *Protomyces andinus*. This is the only station in the vicinity of Madison, Wisconsin, where I have found such infections. However, Dr. J. J. Davis, Curator of the Wisconsin University Herbarium, tells me that he has found them rather commonly in other parts of the state. The galls usually occur near the base of the stem just above the ground, and are roughened knot-like, or more or less fusiform swellings, which may involve the entire circumference or only a sector of the stem. In addition to the galls which occur near the ground still other galls may occur higher up on the stem, in some instances two feet or more above the ground. Galls in these various situations are similar both morphologically and histologically so far as has been observed by the writer.

Before entering into the description and consideration of the gall tissue, it seems well to describe briefly the structure of the normal stem. In the cross section of the gall shown in plate II, figure 8, the fungus has confined its activities to one side of the stem, shown on the upper side of the figure, so that only a sector is involved in gall formation. The bundles on the sides and lower part of the figure are entirely normal. In general there are two sorts of bundles in the normal stem: those in which the xylem is broadly triangular or somewhat aquiliform in cross section, and those in which the xylem forms rather narrow radial segments. The narrow bundles are evidently leaf traces, since six of them leave the stem at each node, and according to Sinnott (5) the trilacunar condition is characteristic of many members of the *Compositae*. The leaf trace bundles are formed two nodes below the point where they leave the stem. There seems to be some difference in the structure of the narrow bundles in the young stem, of which two kinds can be distinguished; but as the normal anatomy is to be considered very briefly, it is beyond the scope of this article to enter into a general investigation of the course of the bundles in the stem. The cambium dips in opposite the narrow bundles (fig. 8), resulting in somewhat depressed segments of xylem. It has on this account a somewhat sinuous course around the xylem ring. The broader bundles usually alternate with the narrow ones, but this is not always true, for sometimes two of the broad bundles occur together. Sometimes a ray extends through the center of a broad bundle, cutting it in two. There is often a slight depression in the center of a broad bundle, causing a notch. A bundle of bast fibers is located opposite this notch, shown by the blackened areas in figure 8. The greater part of the phloem is located just inside the bast fibers. The leaf trace bundles are subtended by somewhat larger bundles of bast fibers.

In the young stem the individual bundles are separated from each other by broad rays which extend from node to node. As the stems grow older and the individual bundles approach each other, the rays become narrower, and shorter vertically. Intangential section (fig. 1), the rays are fusiform and are usually three or four cells wide. They are composed of somewhat angular cells which are elongated in a vertical direction. Uniseriate rays are uncommon. With the exception of the ray cells and vessels the xylem is composed mostly of wood fibers. On the outside of the bast fibers the remainder of the bark is composed of several layers of cortical parenchyma cells which are elongated tangentially. There are also several layers of colenchyma cells, just inside the epidermis, which become thickened opposite the trichomes.

A diagram of a cross section of an infected stem is shown in figure 8. The bundles on the upper side of the stem have become greatly altered through the action of the fungus, while those on the lower part and sides have remained normal in structure. In this instance only a sector of the stem has been involved in gall-formation. The xylem on the infected side has been greatly increased both radially and tangentially, while on the other sides it has only its normal growth. Both the leaf traces and the stem bundles can be recognized on the infected side, as the changes brought about by the fungus in this particular instance are less pronounced than in some other specimens examined. Furthermore, the inner extremities of all the infected bundles have their normal structure, showing that this particular part became infected some time after secondary thickening started. Broad intrafascicular rays have been formed, cutting up the bundles into narrow radial segments of xylem. Masses of parenchyma have formed in the xylem where normally there is no parenchyma. There has also been a great reduction in the number of vessels per unit of area, and the size of the vessel has decreased.

The amount of parenchyma, both ray and wood, and the number and size of the vessels vary greatly in different specimens. The specimen shown in figure 8 is about at a minimum in this respect. In extreme cases the xylem portions of the leaf traces are often suppressed or nearly so, resulting in broad ray-like masses of parenchyma. Where leaf traces fail to appear there are deep notches in the xylem ring, their position being shown externally by longitudinal furrows in the surface of the gall.

The formation of depressed xylem segments is not unknown in normal stems of the Compositae. According to Solereder (7), Schenck has observed a furrowed xylem mass in an undetermined member of the order recalling the structure of the Bignoniaceae. "The furrows in this xylem mass are due to the reduced activity on the part of certain longitudinal strips of the cambium which leads to a smaller production of wood and a proportionally greater development of phloem externally."

It is often the case that the individual bundles disappear entirely and in their place there are masses of parenchyma which show but little distinction between wood and bark. Occasional vessels appear in these masses, and irregularly running strands of cambiform cells.

In this connection it might be well to mention certain peculiar strands of tissue which occur under such conditions. Towards the center of many of the galls, in the region of the pith or in close proximity to the protoxylem portions of the bundles, these strands sometimes appear. They consist of whorl-like arrangements of cambiform cells (fig. 5) which enclose sporanges of the fungus, shown by the dark circles in the figure. Structurally they recall strikingly the tumor-strands described and figured by Smith (6) in stems infected with the crown-gall organism, *Pseudomonas tumefaciens.* Short tracheids sometimes accompany these strands, a condition similar to that described by Smith in some of his strands. They usually extend in a vertical direction but not always for the longitudinal section of one of these strands (fig. 4) also shows cross sections of two other strands. It should be noticed that the strand shown in figure 4 encloses relatively large numbers of the sporanges of the fungus, and that where there are large numbers of sporanges the strand is broader. The line of separation between the strand and the surrounding tissue is sharp, as can be seen in the figure. Near the lower right side of figure 4, a single sporange is shown lying just outside the strand, partly surrounded by cambiform cells, similar to those which make up the strand.

The strands are evidently formed in place near the time of infection and are not a product of later growth which has been pushed in from some other source. This is shown by the fact that in the parts of the gall where they occur all the tissue outside them is very abnormal in structure. That infection takes place while the stems are still very young is evident, for in every gall examined some portion or portions of it showed tissue abnormalities in or nearly to the pith, as well as sporanges of the fungus. Furthermore, there is no indication of crushed cells, or of cells which have been partially absorbed along the course of the strands, such as would probably be the case if the strands represented an invasion from some other source. They are evidently caused by some stimulus emanating from the fungus which brings about active and rapid cell division, but a stimulus which is very local in its effects. It seems to be true in general for this gall that the diffusion zone of the gall stimulus, gall poison, or whatever name we wish to apply to the cause of the gall formation, is very limited in extent. Bundles which are very abnormal in structure and which contain the sporanges of the fungus often occur next to bundles which are entirely normal and free from the fungus. Individual bundles sometimes show abnormalities on one side and nothing but normal tissue on the other. It sometimes happens that strands are formed shortly after secondary thickening has started, and in such cases the protoxylem portions of the bundles are often surrounded by a cambium-like zone of cells.

As the strands occur both in the galls near the ground and in those higher up on the stem, one might expect to find them extending through the intervening normal portion of the stem connecting one gall with another—a condition similar to that described by Smith in the crown gall. Such is not the case, however; they are purely local in their occurrence and extend but little above or below where the infection first took place in the stem. (For a possible explanation of the origin of the higher galls see Stewart, 10.)

The bundles show different degrees of disturbance at different levels. At some level or levels in the gall the tissues are abnormal into or beyond the protoxylem of the bundles and probably represent the places where the fungus first began its activities. Going above or below the level of greatest disturbance the xylem becomes less and less involved, until at the upper and lower limits of the gall only that portion which lies just inside the cambium shows structural abnormalities. Somewhat similar conditions are also found in a peripheral direction, as a larger sector of the stem is involved where the tissue disturbances are deepest than at the upper and lower parts of the gall. This fact is well shown in figure 8, where the inner parts of the bundles are normal. The statements just made are especially true for galls that are fusiform in shape but less true for those which are knot-like, because in galls of the latter type the disturbance is general throughout the greater part of the circumference of the stem.

As a usual thing the cells composing the xylem have an upright position, but occasionally there are cells or groups of cells which are turned over at right angles to their normal position. As was stated earlier in this article, the cambium takes a more wavy course than in the normal stem. This is due to the fact that the central portions of the stem bundles grow more rapidly in the radial direction than do the flanks of the bundles, so that the cambium is bowed outward opposite the central portions (fig. 8). The leaf trace bundles, on the other hand, are often inhibited in their growth and the cambium opposite them extends inward farther than in normal stems. Sometimes the cambium is obliterated for a space, or at least there are no cells which have the form of cambium cells. In cases of this kind it is difficult to find a separation between wood and bark.

The normal phloem (fig. 6) has both sieve tubes and companion cells well marked. Where abnormalities are great in the gall all distinction between sieve tubes and companion cells is lost and the cells have increased enormously in size. Figure 7 was drawn from such tissue and is on the same scale as figure 6. The cambium is towards the lower side in figure 7, and shows the rapid increase in the size of the cells after they are formed. The phloem is here composed of undifferentiated parenchyma which has lost all the characteristics of phloem cells. In longitudinal sections through the phloem there are no indications of sieve plates and the individual cells are about isodiametric. In cases in which the bundles have become infected rather late in their growth there is a mass of normal phloem next the bundles of bast fibers, while that next the cambium is similar in structure to that shown in figure 7.

In the normal stem a bundle of bast fibers usually occurs opposite each fibrovascular bundle. In the gall this is not always true, group of parenchyma cells replacing the bast of fibers. Sometimes in such places the bast fibers are imperfectly formed, in that the walls are thinner and less regular in shape and they still contain protoplasm. These cells are often scattered about through the inner bark and are not arranged in well defined bundles as is the case with normal bast fibers. Well formed fibers sometimes occur among the abnormal ones.

The cortical portion of the bark is usually not greatly changed and as a rule there are but few sporanges in it. The cells often become lengthened tangentially and cross walls form in many of them but otherwise there is no great change. Where the bark has been torn open by pressure from within there are sometimes callus-like masses, but whether these are due to the wound stimulus or to the gall stimulus can not be determined. Irregularly shaped cavities sometimes form in the bark and in other parenchyma portions, evidently due to a breaking down of cells. Somewhat similar cavities also occur in uninfected stems.

A diagrammatic drawing of a tangential section of one of the galls is shown in figure 3. This section shows about average conditions; greater tissue disturbances occur in some galls, in others less. By comparing this figure with that of the normal stem (fig. 1) it is seen that the most striking changes brought about in the gall are the broadening of the rays and a reduction in the width of the bands of fibers and other elements between the rays. There is also a vertical shortening of some of the rays, but this is not especially pronounced. The cells which compose the rays are in general more nearly isodiametric than those in the normal rays, many of whose cells are lengthened vertically. The vessels pursue a more irregular course than in the normal stem, and the vessel segments are much shorter. A sharp turning of the fibers from their usual upright course, which is pronounced in the traumatic wood of this species (fig. 12), occurs but seldom. There are, however, occasional bundle ellipses (fig. 9), which in their more complex form consist of several vessel segments so bent as to form a more or less oval or elliptical body enclosing short tracheids. It is probably true that the larger segments are more nearly like tracheids, as distinct membranes often separate one segment from another. Some of the segments in figure 9 show this condition. Bundle ellipses do occur which are much simpler in structure than the one figured. These sometimes consist of as few as three segments which do not enclose still other cells at the center. Irregularly shaped masses of short segmented vessels also occur variously wound and twisted together.

One gall was found which had been severely wounded. A longitudinal slit had been formed in it extending to within a short distance of the pith. On each side of the wound, parallel with its edges, there are strands of fibers, parenchyma, and short segmented vessels. These have been turned over at right angles to their usual position and extend outward in a radial direction. A small cavity at the inner end of the wound has become surrounded by callus tissue, and a similar modification has taken place along the edges of the wound in the outer bark. Tangential sections through this wounded gall show broad ray-like masses of parenchyma with suggestions of fiber inclusions similar in some respects to the condition found in traumatic wood (fig. 13). Resting as these observations do on a single specimen, it is hardly safe to draw any general conclusions from them. It looks, however, as though the wound stimulus were able in a way to overcome the gall stimulus and to imprint its effect on the tissue formed after wounding, or at least to modify to a certain extent the effects of the gall stimulus.

GALLS OF PAPAIPEMA NITELA ON AMBROSIA TRIFIDA

The stems of *Ambrosia trifida* are often parasitized by the common stem borer *Papaipema nitela* Gn., causing the formation of galls. The galls consist of slight swellings which are often fusiform in shape. The general features of such a gall are shown in the diagrammatic drawing, text-figure 1 A, which represents a gall formed by both Protomyces and apaipema. This being the case, no other drawing was necessary except for special features which are shown in figures 2 and 11.

The structural abnormalities caused by this insect are less striking than those caused by Protomyces. There is a greater radial growth of the xylem portions of the bundles than in the normal stem, leading to the production of a more or less compact woody mass of tissue as shown in the lower part of text-figure 1 A. In this radial growth the bundles lose their individuality as such while they remain separate a short distance above and below the gall. Text figure 1 B is an outline drawing of one of the stem bundles taken just below a gall. The rays are broader, as shown in figure 2, and in some instances there is a great reduction in the number of vessels. There is also a considerable production of parenchyma where normally there are only fibers.

An interesting feature occurs in many of the galls which is shown in figure 11. In many instances it was found that the ray cells had proliferated, forming callus-like masses which extend into the larval chamber. These masses consist of thin-walled parenchyma cells which are often very much elongated. Among the large cells there are still other cells which are very much smaller, and some of these are cambiform and appear to have been recently capable of division. A band of these cambium-like cells often extends across the base of the parenchyma mass and probably is capable of renewing the mass. The cells both large and small are poor in protoplasmic and other contents.

Cosens (1, figs. 17 and 21) shows somewhat similar tissue-masses extending into the larval chamber of two other lepidopterous galls, *Stagmatophora ceanothiella* Cosens on stems of *Ceanothus americanus*, and *Eucosma scudderiana* Clements on stems of *Solidago canadensis*. In the case of the Eucosma gall, at least, he regards these growths as nourishing tissue for the larva, for he states (p. 312): "The gall mass in this case is produced from the vascular bundles and the intervening parenchymatous strands. When the larva first enters the stem it first eats out the pith. After the exhaustion of this source of nourishment, its food is supplied by the radial thickening of the bundles into the gall cavity."

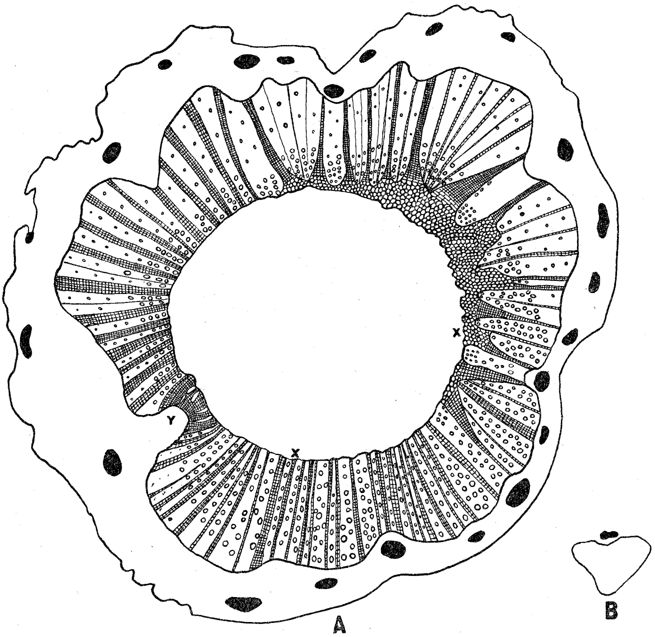
In the gall considered in the present article the cells are very poor in contents which make up the masses, a condition hardly to be expected if they were designed especially as food for the larva. Furthermore, the larva is able to, and does, eat out the pith for a considerable distance beyond where the gall occurs. That they are formed especially for food seems unlikely, as they contain but little substance that could be used for food. The great similarity between these parenchyma masses and callus tissue leads one to suspect that possibly the wound stimulus, resulting from the gnawing of the insect, might have caused them. Indeed, similar instances have already been reported. Küster (3) discusses this phase of the subject at some length. In one instance (p. 279), he states: "Auch in ihren Entwicklungsstadien können die Gallen noch durch Wundreize beeinflusst werden. Im Innern die Potania-Gallen wird das zartwandige Parenchym, das die Larvenkammer auskleidet, und dessen Zellen den Fresswerkzeugen der Gallbewohner zum Opfer fallen, immer wieder durch callusartig Wucherungen regeneriert." There is also a possibility that the callus-like masses result from a stimulus the object of which is to fill the gall cavity with tissue. Küster (p. 314) mentions instances of this kind in which the gall had been abandoned by the insect.

In young galls, where the pith was not entirely eaten away, a ring of cambium-like cells was sometimes found near the border of the cavity. The bundles themselves are sometimes able to proliferate inward, the condition in this respect being similar to that described by Cosens from the gall of *Eucosma scudderiana*. Where conditions of this kind occur there is usually xylem present next the cambium ring, but a short distance inward the character of the cells changes and there is nothing but parenchyma. Sometimes the parenchyma extends to the cambium ring for a considerable space, having entirely replaced the xylem. Bands of cambiform cells occur in these parenchyma masses similar to those which occur in the callus growths already described. They are both eaten by the larva to some extent, but it seems unlikely that they are formed by the plant for this purpose through some stimulus from the larva.

GALL OF PROTOMYCES ANDINUS AND PAPAIPEMA NITELA ON AMBROSIA TRIFIDA

In the thicket from which the Protomyces galls described in this article were taken there were also plants of *Ambrosia trifida* which bore galls of *Papaipema nitela*. I was fortunate enough to find several galls in which both fungus and insect were present, and from the structure of these it was evident that both organisms had contributed to their formation. In some of these galls the fungus was confined to a sector of the stem, as was shown by the presence of the sporanges in this part only. From facts already mentioned in this article, we can safely assume that the opposite side of the gall, which contained no sporanges, had not been influenced by the fungus in its development. A diagrammatic drawing of a cross section of one of these galls is shown in text-figure 1. On the lower side of the figure, between the letters X-X, there is a sector, including about one fourth of the stem, which has no sporanges or other indications of the fungus in it. The remainder of the section has the fungus present in it to a greater or less extent.

The structure of the portion on the lower right side is similar to that of galls formed entirely by the insect. There is a greater radial growth of the bundles, as can be seen by comparing the width of the bundles with that of a normal bundle from the same stem (text-figure 1 B). The radial growth of the bundles is often more than twice normal. The inner extremities of the bundles have been eaten away in all but two cases, on the right side just below X where a small part of the pith remains. The bark on this part of the gall is but slightly thickened, being similar in this respect to galls which are formed entirely by the insect. To the left and above the area indicated by the letters, all the tissues of the stem have come under the influence of the fungus to a greater or less extent. The invasion of the fungus has been slow in a peripheral direction, and the inner ends of several bundles, on each side of the area X-X, show the characteristic structure of the xylem of the insect gall. The structure of the outer parts of the bundles, on the other hand, shows abnormalities commonly found in the Protomyces gall, especially the greater production of parenchyma and the reduction in number and size of the vessels. A deep depression occurs on the lower left side, at Y, caused by the suppression of one of the leaf trace



TEXT-FIG. 1. *A*, Diagram of a cross section of a gall formed by *Protomyces andinus* and *Papaipema nitela* (× 27). *B*, outline of a single bundle taken from a section just below the gall (× 27). Description of both drawings in text.

bundles. This area is filled with a mass of parenchyma in which there are a few fibers but no vessels. There is a slight proliferation of the parenchyma into the gall cavity similar to that which has been described from the insect gall. There are no fungus sporanges immediately adjacent to this proliferation, but they do occur close to what was formerly the cambium. Opposite the parts occupied by the fungus the bark is very irregular and thickened, as can be seen by comparing the two sides of the figure.

We have well illustrated in this gall the effects of the two stimuli, fungus and insect, working together. Of the two, the stimulus from the fungus seems to be the stronger. In portions of the stem where the fungus was present very early in the growth of the bundles, all the structural characteristics are present which are commonly found in galls formed by the fungus alone. On the side of the stem where the fungus was not present in the early growth the structure is the same as in the insect gall. As the fungus spreads in a peripheral direction, however, those bundles which have already responded to the stimulus from the insect in their early growth immediately assume the structure of the fungus gall in the tissue formed after invasion. When the two stimuli act together on young tissue it seems to be true that only that from the fungus is capable of causing change in structure. When the fungus invades tissue already under the influence of the stimulus from the insect, the influence of the latter is destroyed or neutralized and the tissue formed subsequently is that of the fungus gall.

It is unfortunate in this case that we have to do with an insect gall former which is incapable of causing violent disturbances in the host plant. It would be interesting to know what would be the result on the tissues of the host plant if two organisms, a fungus and an insect both capable of producing profound tissue modifications, should exert their influence at the same time.

Traumatic Wood of Ambrosia Trifida

It is beyond the scope of this article to enter into a description of the various types of traumatic wood which result from the different kinds of wounds such as has been given by deVries (2) and Mäule (4), because only general features of the traumatic tissue are of interest in this connection. It might be well to mention, however, that the types of wound wood examined are quite similar in a general way to types described by these authors.

Wood resulting from two sorts of wounds was examined. One of the wounded stems was collected along a roadside where a vehicle or some other moving object had torn away one side of the stem which had later started to heal over. The other was of a stem which had been broken over and badly twisted. The first of these stems was examined from cross and tangential sections, the second from tangential sections only. The cross section of the first shows a solid mass of wood in the wounded area, 8 mm. thick at the widest point, which had lost all appearance of having come from a stem normally herbaceous. The vessels are smaller than in the normal stem and are reduced in number. With the exception of occasional broad ray-like masses of parenchyma, the rays are but little broader as a whole than they are in the normal stem. In tangential section the rays are shortened vertically. As a whole there is less ray tissue per unit of area than in the normal stem (fig. 12). There are occasional broad ray-like masses of parenchyma (shown by the heavy lines in the ray, fig. 13), which call to mind very strikingly the similar condition that has been described in the rays of some of the lower angiosperms. The vessel segments are much shortened (compare figs. 1 and 12). The only features worthy of special mention found in the stem which had been twisted are the bundle ellipses, one of which is shown in figure 10. They are very similar to the bundle ellipses in the Protomyces gall (fig. 9).

General Summary

After having considered the structural changes brought about in the Ambrosia stem through the action of the different stimuli treated in this article, it seems desirable to give a brief comparison and summary of the results. One of the more marked features of pathologic plant tissue is the change in general direction of the cells, and in the cases being considered this is more marked in the truamatic wood. An interesting thing in this connection is the fact that the changes brought about by wounding are about the same as those which occur in traumatic tissue of the lower angiosperms. An examination of the literature has revealed practically nothing concerning the structure of wound tissue in the Compositae. A great misplacement of xylem cells takes places, as a result of which they are often 90° or more from their normal position. Gnarl-formations and similar structures result from such misplacements, the bundle ellipses being a marked feature in this respect. With few exceptions the cells in the Protomyces gall occupy more nearly their normal positions and there is but little of the violent misplacement so common in traumatic wood. There are, however, occasional gnarl-like arrangements of cells, best illustrated by the bundle ellipses which are very similar in structure to those of traumatic wood. The insect gall shows no marked misplacement of cells.

Another characteristic feature is the production of parenchyma at the expense of the xylem, a feature which is more marked in the Protomyces gall than in any other. In extreme cases considerable portions of the xylem may be converted into parenchyma. Broad ray-like masses of parenchyma are a constant feature in certain types of traumatic wood. Intermixed with the ray tissue there are often fibers singly or in groups. In the insect gall the production of additional parenchyma tissue is chiefly confined to the proliferation of the ray cells into the gall cavity.

The rays show the greatest alteration in the Protomyces gall, where they are much broader, and the intervening strips of fibers and other elements are narrower than in normal tissue. There is, furthermore, but little vertical shortening of the rays. In traumatic wood, on the other hand, there is a marked vertical shortening of the rays, a feature common to the traumatic wood of most species of angiosperms. The insect gall shows but little alteration in ray structure.

The number and size of the vessels is also greatly influenced by the different stimuli in question. The reduction in number is very marked in both traumatic wood and Protomyces gall, but in the insect gall there is very little change in this respect. There is a noticeable shortening of the vessel-segments in all the types of pathologic tissue under consideration.

As regards the effect of the different stimuli acting together, the insect is able to exert an influence on the growth in all parts of the stem which are in close proximity to the insect. The fungus, on the other hand, is able only to influence growth where the fungus is actually present in the tissue. The insect is therefore able to exert an influence much farther away from the source of the stimulus than is the fungus. When both parasites occupy a portion of the stem at the same time, the insect is able to influence the growth on all sides of the stem from the start, while the stimulus from the fungus is limited owing to the relatively slow spread of the fungus through the tissues. In places where the application of the two stimuli evidently began at about the same time the resulting tissue is the same in structure as that which occurs in the Protomyces gall, the stimulus from the insect being apparently inactive under such conditions. In portions free from the fungus the changes are the same as are usually found in the insect gall. If the fungus extends into such tissue, however, there is an abrupt change in the tissue formed afterwards, this tissue having the same structure as in the Protomyces gall. From these facts we may conclude that the stimulus from the fungus is much the stronger of the two and is able to overcome or neutralize the stimulus from the insect.

Observations on wound and fungus stimuli acting together rest on too few observations to warrant any definite conclusions. It is likely, however, that the wound stimulus is more powerful than the gall stimulus; this at least is suggested by certain modifications in the wounded gall examined. This conclusion is further substantiated by the fact that in general the gall stimulus is not effective for any great distance away from the source of the stimulus, while in the case of the wound stimulus tissue modifications take place at considerable distances from the wound.

The most marked similarities between the structure of the fungus gall and that of traumatic wood are in the presence of bundle ellipses and in the reduction in the number and size of the vessels. Similarities between the insect gall and traumatic wood consist in a greater radial growth of xylem, resulting in a more distinctly woody growth than takes place normally.

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EXPLANATION OF PLATE II

All drawings are from the stem of *Ambrosia trifida* L. Figures 4, 5, 6, 7, 9, 10, and 11, show detailed structure. Because of the low magnification the remainder of the drawings are diagrammatic.

FIG. 1. Tangential section through wood of normal stem. × 28.

FIG. 2. Tangential section through gall of *Papaipema nitela*. × 28.

FIG. 3. Tangential section through gall of *Protomyces andinus*. × 28.

FIG. 4. Longitudinal section through gall of *Protomyces andinus* showing structure of tissue strands. × 133.

FIG. 5. Cross section of tissue strand from gall of *Protomyces andinus*. × 133.

FIG. 6. Cross section of normal phloem. × 133.

FIG. 7. Cross section of phloem of gall of *Protomyces andinus*. × 133.

FIG. 8. Cross section of gall of *Protomyces andinus*. The upper portion alone shows abnormalities. × 6.

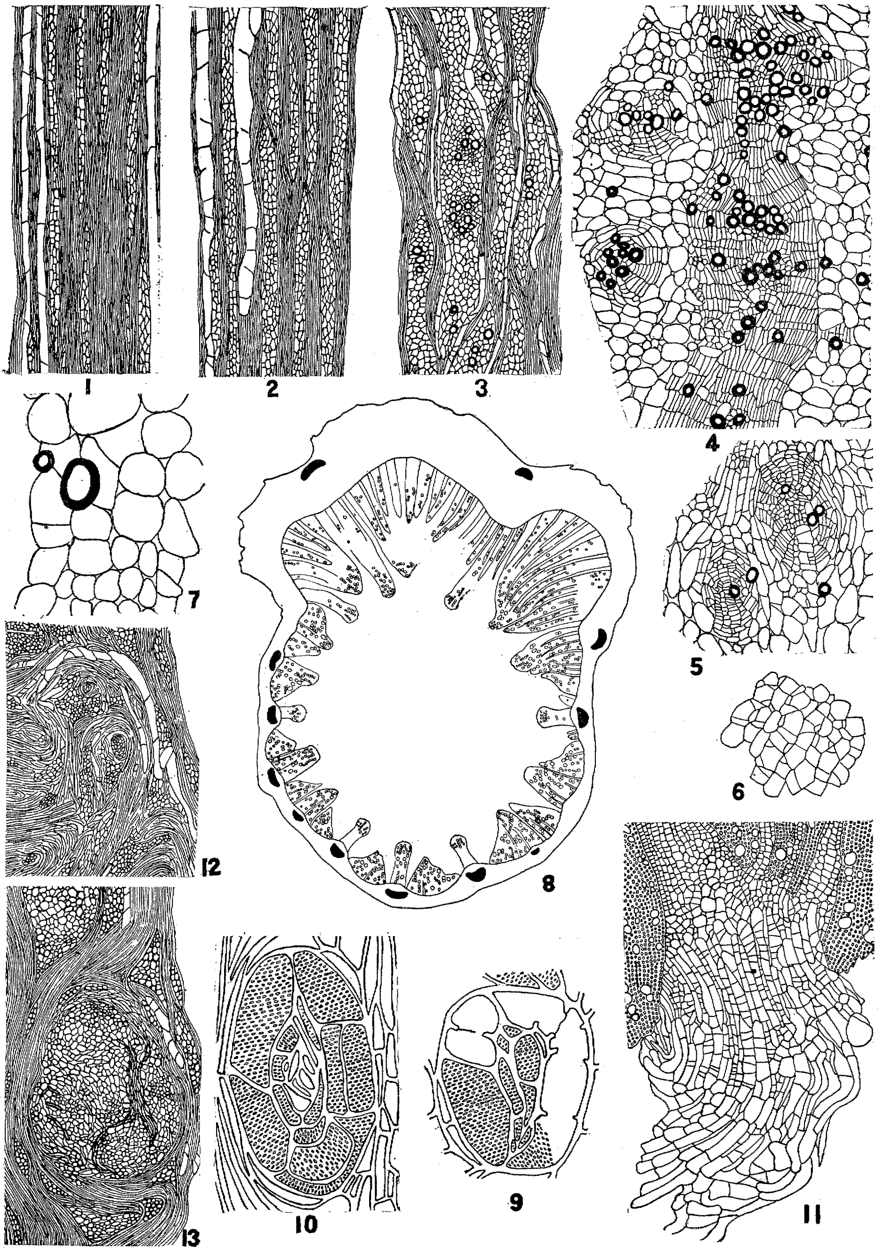
FIG. 9. Bundle ellipse from gall of *Protomyces andinus*. × 133.

FIG. 10. Bundle ellipse from traumatic wood. × 133.

FIG. 11. Proliferation of ray tissue into gall cavity in gall of *Papaipema nitela*. × 133.

FIG. 12. Tangential section through traumatic wood showing course of fibers and vessels. × 28.

FIG. 13. Tangential section through traumatic wood showing fiber inclusions in the broad rays. × 28



STEWART: PATHOLOGIC CONDITIONS IN AMBROSIA TRIFIDA.